



Evaluation of changes in macrobenthic standing stock and polychaete community structure along the south eastern Arabian Sea shelf during the monsoon trawl-ban

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ABSTRACT

The south eastern Arabian Sea is characterized by moderate coastal upwelling, high biological production and subsurface oxygen depletion during the southwest monsoon (June–September). Concurrently, a seasonal closure to trawling activities (15th June–31st July) is implemented here, as a sustainable ecosystem management practise. The effects of monsoon driven environmental changes and consequences of trawling cessation on macrofauna were assessed, based on surveys at 12 sites (30–200 m) preceding and during different phases of the southwest monsoon. Macrofaunal density and biomass increased considerably towards the mid and late monsoon along the inner shelf (30–50 m) where trawling is intense, while no temporal changes were observed along the outer shelf (100–200 m). Density increased four-folds at the 30 m contour and three-folds at 50 m, while biomass nearly doubled at both depths, reflecting a marked increase in density of polychaetes (61–87% of macrofauna). The disproportionate increase in faunal density and biomass along the inner shelf (30–50 m) was due to abundance of juvenile polychaetes and dominance of small-sized opportunists towards late monsoon (August–September). A concurrent hike in nominal species count of polychaetes was also observed in the study area. The increase in polychaete standing stock and high density of planktonic larvae during onset and peak monsoon, coupled with occurrence of juveniles as well as gamete-bearing adults in sediments, indicates that the southwest monsoon is a peak breeding season for the dominant polychaetes in the region. The trawl-ban during this period facilitates the recoupment of benthos by maximising spawning success and larval settlement, thereby enhancing overall ecosystem integrity.

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1. Introduction

Benthic communities, composed of complex assemblages of organisms living in association with sea-floor sediments, play a central role in the functioning of marine ecosystems (Koho et al., 2013). Benthic fauna are of primary importance in the assimilation of the substantial quantities of organic matter settling on the seafloor, which are transferred to benthic and pelagic food webs via trophic interactions. Soft bodied benthic fauna are important sources of food for diverse demersal fishes and shellfish; and in most cases, economically exploited fishery resources are supported in regions with high benthic biomass (Crisp, 1984; Snelgrove, 1998). Bioturbation by benthic fauna increases oxygen

penetration in sediments and enhances the degradation of organic matter (Mermillod-Blondin, 2011). The integrity of the benthic realm is critical in overall ecosystem functioning as well as in supporting fishery resources. Being sessile or with limited mobility, benthic fauna are particularly vulnerable to physical, chemical and ecological disturbances.

The continental shelf off Kerala state in the southwest coast of India is known for its commercially exploited finfish and crustacean resources. Bottom trawling is the most common fishing activity, with ~4000 trawlers operating along the state's coastline (595 km), resulting in high fishing pressure (Naomi et al., 2011). Scientific evaluations have raised concerns about the presumed damages to benthic habitats by trawling gears (Bergman and Hup, 1992; Collie et al., 2000; Kaiser et al., 2006; Queirós et al., 2006; Tillin et al., 2006). Direct effects of bottom trawling include scraping and ploughing of the substrate, sediment resuspension and destruction of benthic assemblages. Indirect effects include

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post-fishing mortality of benthos and long-term trawl-induced changes in benthic community structure. Such long term changes may affect food availability for commercially important fishes and may also modify demersal food webs (Jennings and Kaiser, 1998; Jennings and Reynolds, 2000; Kaiser et al., 2006; Kumar and Deepthi, 2006). A handful of experimental studies have been undertaken to understand immediate changes in benthos after trawling off Kerala and other parts of the Indian coast (Thomas et al., 2006; Zacharia et al., 2006; Bhagirathan et al., 2014).

Concern over the ecosystem effects of fishing has led several countries to close parts of the sea bottom to mobile fishing gear for preserving ecosystem function and fish production (Kaiser et al., 2002). A closed fishing season for mechanised trawling vessels is implemented in all coastal states of India as well, with the view of reducing fishing effort during peak spawning periods of commercially important species, and also to reduce stress on the benthic fauna (Vivekanandan et al., 2010). The ban period along the Kerala coast, in the South Eastern Arabian Sea (SEAS) is between 15th June and 31st July (Kerala Marine Fishing Regulation Act, 1980) each year and coincides with the onset of the southwest (summer) monsoon, during which moderate to intense coastal upwelling occurs in the region (Smitha et al., 2008), resulting in enhanced biological production (Habebrehman et al., 2008) and sub-surface hypoxia (Banse, 1959; Naqvi et al., 2009).

The trawling ban off Kerala during the monsoon season is generally considered to be an effective practise from the perspective of sustainable resource management (Vivekanandan et al., 2010). Though the quantitative and qualitative distribution of macrobenthos of the SEAS shelf is well described (Jayaraj et al., 2008; Joydas and Damodaran, 2009, 2014), reports on the impacts of trawling cessation on benthos are limited (Thomas et al., 2006). The temporal change in macrobenthic standing stock and composition during the monsoon upwelling, when the region is characterized with high production, increased organic matter (OM) flux and bottom water hypoxia, has not been addressed in an integrated manner for the sizeable SEAS shelf as a whole.

Based on surveys preceding (May, pre-monsoon and June, monsoon onset) and following the trawl-ban (August, peak monsoon and September, late monsoon) in the SEAS shelf (~7–9°N, 30–200 m), this investigation aims to: (i) study changes in standing stock and composition of benthic macrofauna, as well as community structure of polychaetes during the southwest monsoon, and (ii) determine whether breeding of polychaete taxa in the region coincides with the monsoon (through examination of meroplankton). The changes in quantum and composition of macrofauna across the monsoon season are considered from the perspective of the trawl-ban.

2. Materials and methods

2.1. Study area

The present study focuses on the continental shelf (30–200 m) of the southern part of the SEAS, between ~7° and 9°N latitudes. The SEAS is subjected to seasonal wind reversal associated with the southwest (summer) monsoon (June–September) and north-east (winter) monsoon (November–February), which influences the hydrography and oceanography of the upper water column (Smitha et al., 2008). As a result of constant influences from the equatorial Indian Ocean and the less saline Bay of Bengal, salinity is relatively low in the study area, when compared to the rest of the eastern Arabian Sea (Prasannakumar et al., 2004). During the southwest monsoon, moderate to intense coastal upwelling occurs in the SEAS, with isotherms tilting upwards from around April (Smitha et al., 2008). This causes nutrient enrichment in the upper

water column, which results in enhanced biological production in the euphotic zone (Madhupratap et al., 2001). The high production and terrestrial runoff during this season, coupled with strong stratification, results in rapid utilisation of dissolved oxygen and formation of seasonal sub-surface hypoxia over the SEAS shelf (Naqvi et al., 2009).

The high seasonal production also enhances finfish and crustacean resources in the SEAS, which are subject to intense year-round fishery (Silas, 1977; Suseelan and Pillai, 1993), except during the 45-day trawl-ban period (June–July). Intense prawn fishery (using otter trawls) is practiced in the grounds lying between Kayamkulam (near Kollam) and Anjuthengu (near Trivandrum) and off Cape Comorin (Naomi et al., 2011). Single-day trawling operations in the region are restricted to ~30–50 m water depth, while multi-day operations are focused even beyond 100 m depths (Naomi et al., 2011). In general, the smooth topography of the mid-shelf region of the SEAS proves ideal for trawling. There is considerable concern about the extremely high fishing pressure in the SEAS shelf (Vijayan et al., 2000).

2.2. Sampling

Four surveys were undertaken in the study area on board Fishery Oceanographic Research Vessel *Sagar Sampada* – during June 2009 (FORVSS 267: pre-ban, monsoon onset phase/OP), August 2009 (FORVSS 270: post-ban, monsoon peak phase/PP), May 2010 (FORVSS 275: pre-ban, pre-monsoon/ PM) and September 2011 (FORVSS 289: post-ban, monsoon late phase/LP) to assess macrofaunal standing stock and composition.

During the first two surveys (OP and PP 2009), samples and data were collected at 12 sites (Fig. 1), located at 4 depths (30, 50, 100 and 200 m) in 3 transects along 77°30'E (N–S off Cape Comorin, CAP), 8°30'N (E–W off Trivandrum, TVM) and 9°N (E–W off Kollam, KLM). A modified Smith–McIntyre Grab (0.2 m²) was deployed to collect surface sediment samples at each site in duplicate. A sub-sample for sediment texture and organic matter analyses was collected from the grab and oven-dried (at 55 °C). The remaining sediments from the grab were sieved on-board, through a 500 µm mesh, and the retained materials were preserved in 5% buffered formaldehyde solution containing Rose Bengal stain. Sampling was rendered impossible at the 200 m station off Cape Comorin during the first survey, owing to bad weather. The sites between 30–100 m along TVM and KLM transects were revisited during the PM and LP surveys (while operational limitations made sampling at 200 m impossible). The above procedure was followed to collect macrofauna, with the use of a 300 µm mesh instead of 500 µm. Since smaller-sized fauna were found to dominate in the OP and PP samples and are reported to be important components of macrofauna below upwelling systems including SEAS (Abdul Jaleel et al., 2014), the smaller sieve was used in the latter surveys (PM and LP), so as to better quantify changes in standing stock across the southwest monsoon, including the contribution of smaller individuals. A total of 60 grab samples were collected during the entire study. A conductivity temperature depth (CTD) profiler (SBE 911-Plus) was used to record salinity and temperature at all sites, and water samples were collected in the attached rosette sampler for estimation of dissolved oxygen in near-bottom water following Winkler's Method (Strickland and Parsons, 1972).

In order to examine quantitative and qualitative composition of polychaete larvae in the water column, zooplankton samples were also collected during three cruises in June, August and September 2009 (FORVSS 267, 270 and 272), which corresponded to onset (OP), peak (PP) and late phases (LP) of the southwest monsoon. During each cruise an oblique surface Bongo net (300 µm mesh) haul at the surface and a vertical Multiple Plankton Net (MPN,

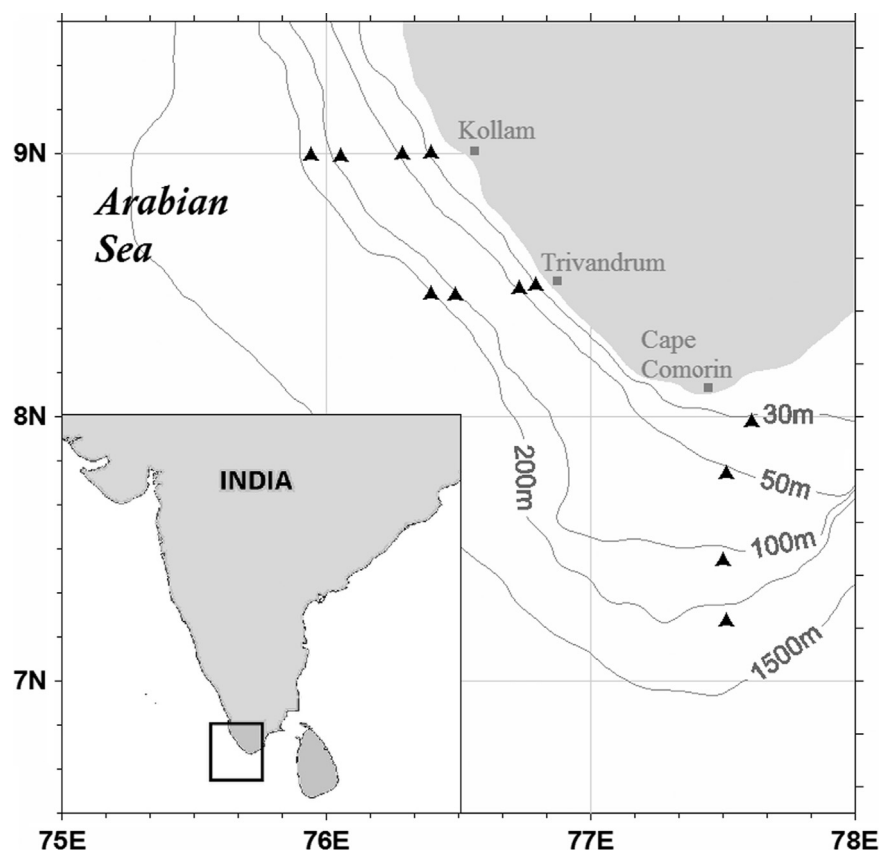


Fig. 1. Map of the south eastern Arabian Sea showing bathymetry and location of sampling sites.

200 μm) haul (entire water column) were done at each of the 12 study sites.

2.3. Sample analysis

In the shore lab, the preserved grab samples were again sieved (using 500 μm mesh for OP and PP samples and 300 μm mesh for PM and LP samples) and the macrobenthic organisms were sorted to group level (polychaetes, crustaceans, molluscs and others). The wet-weight biomass of each group was taken using a Mettler Toledo (AB204-S, ± 0.1 mg accuracy) electronic balance (biomass of molluscs was taken shell-on). The polychaetes of the OP and PP surveys were identified to the species level, using standard identification keys (e.g.: Day, 1967; Fauchald, 1977). Simultaneous with taxonomic identification, the maturity stages of polychaetes were also taken into account, and mature adults bearing ripe gametes were noted. Meroplanktonic polychaetes collected in the bongo net and MPN were also sorted to family level using standard keys (e.g. Crumrine, 2001; Rouse and Pleijel, 2001; Rodriguez-Valencia 2003). For uniformity in quantification, the larval abundance was standardized to $\text{ind.}10\text{ m}^{-3}$ of water.

Sediment texture analysis was done on the dried sub-samples using a Particle Size Analyser (Sympatec) and expressed as percentage of constituent classes – sand, silt and clay following the nomenclature of Shepard (1954). Organic carbon content of the sediments (dried and pulverised) was estimated through the wet oxidation method (El-Wakeel and Riley, 1957), and converted to percentage of organic matter (OM) in (dry weight of) sediments following Trask (1939).

2.4. Statistical analyses

Significance of spatial and temporal variations of

environmental parameters and standing stock of macrofaunal groups were tested using analysis of similarity (ANOSIM in PRIMER-6) employing Euclidean distance on log transformed, normalised environmental data and average ranked values of Bray–Curtis similarity in square root-transformed biological data. Univariate diversity measures of polychaete assemblages were calculated to determine spatio-temporal variations in community structure. Species richness was measured as a direct count of number of species in each sample (S), while the Shannon–Weiner diversity index ($H'_{\log 2}$) was employed to account for the relative abundance of species in each sample. The Simpson's index (λ') was used to determine relative dominance of species at each site. The ratio of biomass (in mg) to the density of polychaetes at each depth stratum was calculated, as an index of body size. The shift in density and dominance of certain polychaete families was visualised by superimposing bubbles of their density on non-metric multi-dimensional scaling (nMDS) ordinations of square-root transformed species abundance data.

3. Results

3.1. Sediment characteristics and hydrography

Significant bathymetric heterogeneity (ANOSIM $R=0.367$, $P=0.1\%$) in sediment characteristics was noticed in the OP and PP surveys (Fig. 2). Sand was the predominant textural class (56.9% to 100%), while contributions of silt (1% to 32.6%) and clay (0.4% to 10.6%) were relatively low at all stations except KLM-30 (30 m off Kollam). Here, clay was the major component (silt 20.6% and clay 68.8%) during the OP survey, while the proportion of silt increased considerably in the PP (silt 46.2% and clay 47.4%). Sediment texture at all other sites remained more or less unchanged between OP

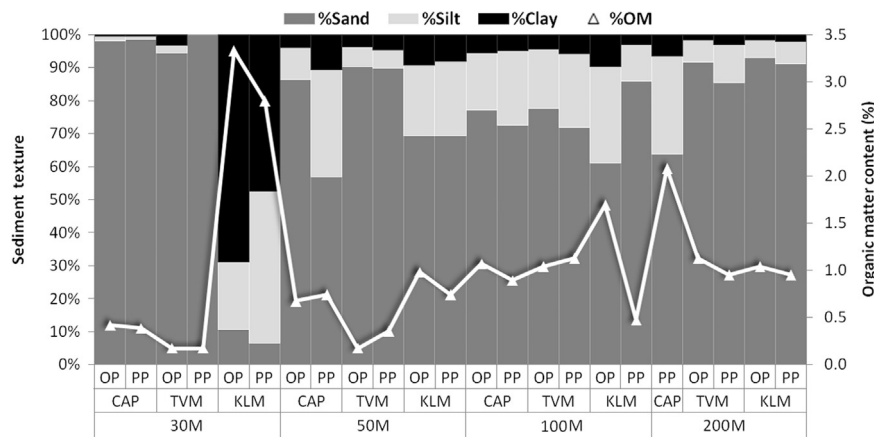


Fig. 2. Sediment texture (vertical stack showing percentage composition of sand, silt and clay) and organic matter (OM) content (line graph showing % of sediment dry weight) at the sampling sites during onset (OP) and peak (PP) phase of the southwest monsoon.

and PP (Fig. 2).

Organic matter was relatively low, varying from 0.18% to 3.33%. Highest OM values were recorded at KLM-30, where proportion of fine sediments was exceptionally high. The content of OM increased towards the shelf edge (Fig. 2) in both surveys, but significant temporal change was not noticed. At KLM-100, OM decreased remarkably from OP to PP, and reflected changes in sediment texture (sand fraction increased by 25% and silt decreased by 19% in PP). The OM content was found to be strongly correlated with silt ($r=0.683$, $p<0.001$) and clay ($r=0.846$, $p<0.001$) content of sediments.

Bottom temperature recorded a drop ($0.36\text{--}2.04\text{ }^{\circ}\text{C}$) during the PP and DO fell close to 0.2 ml l^{-1} at all stations except at CAP-30 and CAP-50 (1.63 and 1.25 ml l^{-1} , respectively). This was an indication of upwelling, which had been initiated during the OP and was well established in the entire study area in the PP, with a slight relaxation in the CAP transect (Thomas et al., 2013). The mean values of bottom water salinity, temperature and DO and sediment characteristics at each depth stratum during OP and PP are given in Table 1.

3.2. Standing stock and composition of macrofauna

The mean ($\pm$ SD) density of macrofauna ($>500\text{ }\mu\text{m}$) in the study area during OP was $1112 \pm 606\text{ ind m}^{-2}$, while during the PP it increased to $1932 \pm 1726\text{ ind m}^{-2}$. The mean biomass did not vary significantly from OP ($5.82 \pm 3.53\text{ g}^{-2}$) to PP ($6.94 \pm 6.21\text{ g}^{-2}$). During both surveys, mean macrofaunal density and biomass were highest at the 50 m sites (Fig. 3a and c). Along the inner shelf (30 and 50 m), marked increase was noted in both density ($R=0.44$, $P=0.6\%$) and biomass ($R=0.27$, $P=2.6\%$) of macrofauna towards the PP, while significant variations were not

observed at deeper sites (100 and 200 m). The hike in density was over four folds at the 30 m contour and nearly three folds at 50 m, while biomass nearly doubled at both depths (See Appendix).

Polychaetes were the dominant group in the region, contributing 57% to density and 38% to biomass in the OP, which increased to 87% and 55% respectively during the PP (Fig. 3a and c). The marked increase in macrofaunal density along the inner shelf was a reflection of increase in polychaete abundance (PP). The contribution of polychaetes to total density increased from 63% to 89% at 30 m and from 60 to 86% at 50 m. There were no significant changes in standing stock of polychaetes at the 100 and 200 m sites (See Appendix).

Crustaceans were the second most abundant group, contributing 26% to mean density and 34% to mean biomass in the OP (Fig. 3a and c). While the density and biomass of this group decreased marginally in the PP, their contribution to total standing stock recorded a drastic drop, representing 8% of density and 14% of biomass. The decline in abundance of this group was more prominent at the 100 and 200 m contours, and crustaceans were altogether absent along the 200 m sites off Trivandrum and Kollam during the PP. Molluscs, which were sparsely represented during the OP, displayed an overall increase in standing stock towards the PP (See Appendix).

Comparisons of macrofaunal ($>300\text{ }\mu\text{m}$) standing stock off Trivandrum and Kollam (30–100 m) revealed a sharp increase from pre-monsoon (PM) to the late phase (LP) of the monsoon (Fig. 3b and d). This temporal change was most noticeable at the 50 m contour (2558 ± 1290 to $7559 \pm 2003\text{ ind m}^{-2}$), where polychaete density recorded a five-fold increase (1368 ± 1305 to $6326 \pm 1879\text{ ind m}^{-2}$) and crustaceans also increased in numbers (595 ± 7 to $950 \pm 78\text{ ind m}^{-2}$). At the 30 m contour also, density of macrofauna (5100 ± 2722 to $7365 \pm 4633\text{ ind m}^{-2}$) increased

Table 1

Environmental parameters (mean $\pm$ SD) at the four depth strata during the onset and peak phases of the southwest monsoon.

		Onset phase (OP)				Peak phase (PP)			
		30 m	50 m	100 m	200 m	30 m	50 m	100 m	200 m
Bottom water characteristics	Salinity	34.99 ± 0.01	34.95 ± 0.03	34.90 ± 0.02	35.01 ± 0.01	34.98 ± 0.06	34.95 ± 0.06	34.92 ± 0.07	34.99 ± 0.01
	Temperature ($^{\circ}\text{C}$)	24.08 ± 0.76	22.17 ± 0.51	19.31 ± 0.66	13.96 ± 0.44	22.67 ± 1.09	21.89 ± 0.97	16.71 ± 2.24	13.84 ± 0.42
	Dissolved oxygen (ml l^{-1})	1.22 ± 0.26	0.77 ± 0.13	0.45 ± 0.07	0.26 ± 0.03	0.68 ± 0.83	0.55 ± 0.61	0.21 ± 0.02	0.23 ± 0.02
Sediment characteristics	Sand (%)	67.8 ± 49.5	82.0 ± 11.2	72.0 ± 9.4	92.4 ± 1.1	68.3 ± 53.6	72.0 ± 16.7	76.9 ± 8.0	80.1 ± 14.5
	Silt (%)	8.0 ± 10.9	12.4 ± 8.2	21.5 ± 6.7	6 ± 1.2	15.7 ± 26.4	20.3 ± 13.6	18.6 ± 6.7	16.1 ± 12.1
	Clay (%)	24.2 ± 38.6	5.6 ± 3.0	6.5 ± 2.8	1.6 ± 0.1	15.9 ± 27.3	7.7 ± 3.1	4.6 ± 1.4	3.8 ± 2.3
	Organic matter content (% sediment dry wt.)	1.3 ± 1.8	0.6 ± 0.4	1.3 ± 0.4	1.1 ± 0.1	1.1 ± 1.5	0.6 ± 0.2	0.8 ± 0.3	1.3 ± 0.7

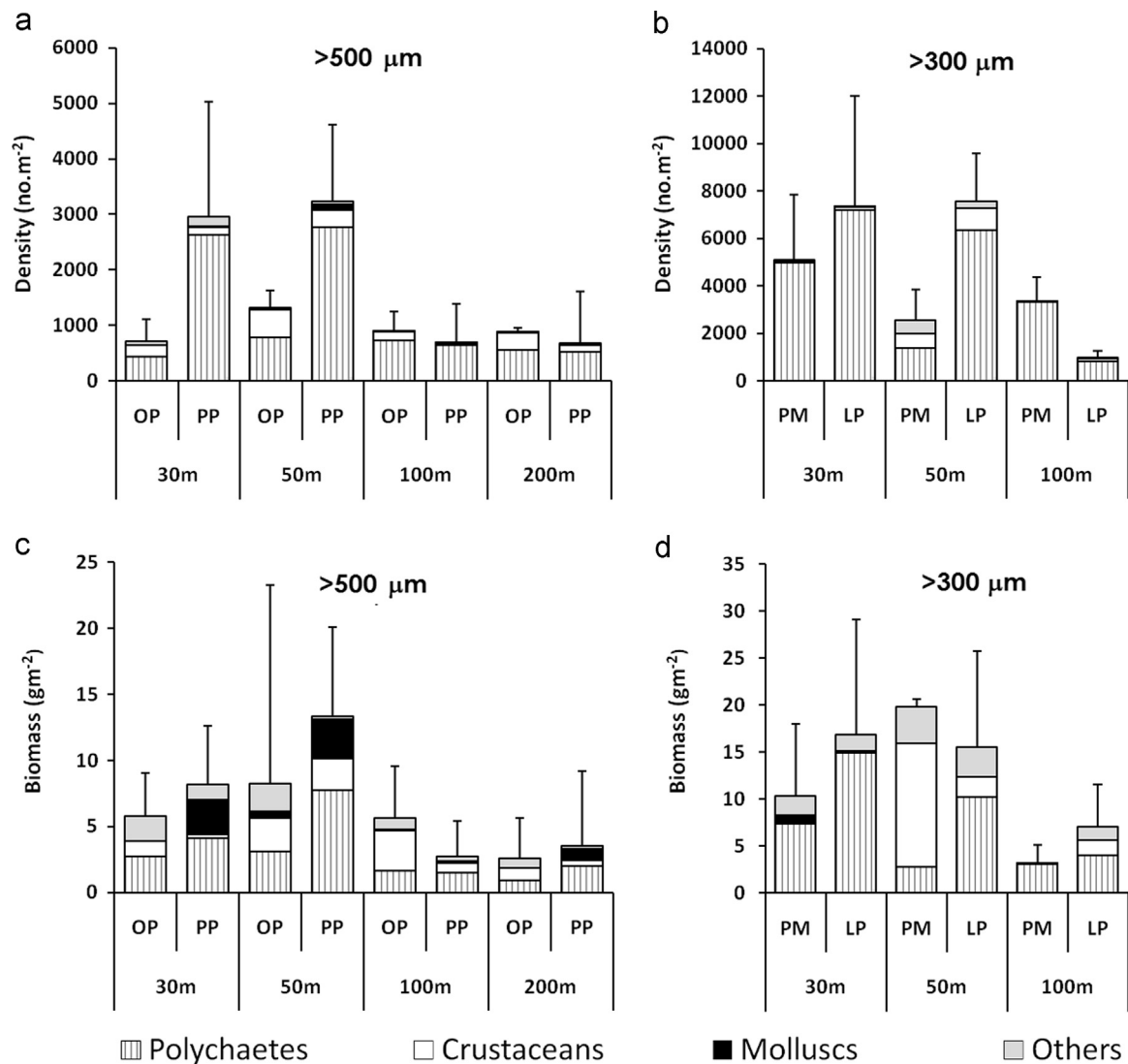


Fig. 3. Mean density and biomass of macrofaunal groups at each depth stratum during the pre-monsoon (PM), onset (OP), peak (PP) and late phase (LP) of the southwest monsoon. (a) mean density (> 500 µm): OP and PP, (b) mean density (> 300 µm): PM and LP, (c) mean biomass (> 500 µm): OP and PP and (d) mean biomass (> 300 µm): PM and LP. Bar provides means for total macrofauna and line represents standard deviation for total macrofauna.

markedly, owing to increase in polychaetes (4950 ± 2652 to 7175 ± 4548 ind m^{-2}) and crustaceans (75 ± 35 to 170 ± 71 ind m^{-2}). Comparable changes were noted in biomass of polychaetes at 30 m (7.33 ± 6.35 to 14.91 ± 9.92 ind m^{-2}) and 50 m (2.81 ± 1.23 to 10.25 ± 8.12 g m^{-2}). Significant temporal changes were not observed in standing stock between PM and LP along the 100 m contour.

3.3. Composition and diversity of polychaetes

A total of 189 polychaete species belonging to 43 families were identified from the region during the OP and PP (2009). The numerically abundant families amongst these were Spionidae (55%), Cirratulidae (5%), Paraonidae (5%) and Pilargidae (4%). The abundance and relative composition of spionids increased drastically in the PP (40–61%), and was most prominent along the inner shelf (Fig. 4a). A considerable increase in abundance of cirratulids, pilargids and ampharetids was recorded at 50 m sites, while most of these families (except Spionidae and Cirratulidae) showed a decrease in abundance at 100 and 200 m (Fig. 4). During the OP, the dominant species in the SEAS shelf were *Paraprionospio pinnata* (11%), *Prionospio* sp. 1 (10%), *Prionospio* spp. (8%) and *Notomastus*

sp. 1 (6%); and the relative proportion of these species changed to 11%, 29%, 13% and 1% respectively in the PP. A set of 19 species chiefly representing Spionidae, Capitellidae, Cirratulidae, Magelonidae and Pilargidae accounted for 61% of polychaetes during OP and 75% during PP. The mean densities of polychaete families at each depth stratum during the OP and PP are given in Appendix.

Nominal species count of polychaetes (*S*) ranged between 8 and 96. It increased from the OP to PP along the inner shelf (except KLM-50) and decreased drastically towards the outer shelf (Fig. 5a), particularly off Trivandrum and Kollam. A clear latitudinal (transect-wise) and bathymetric trend was also noted, with higher values in the inner shelf and towards the south (CAP). Despite the increase in species richness along the inner shelf, species diversity ($H' \log_2$) decreased in the PP (Fig. 5a). Along the outer shelf also, an increased dominance and low diversity was observed in the PP (Fig. 5a and b). The increase in density and high dominance of Spionidae (*Paraprionospio* sp.1, *Prionospio* spp.), Ampharetidae (*Ampharete* spp.), Cirratulidae (*Tharyx* spp.) and Magelonidae (*Magelona* spp.) in the PP, particularly along the inner shelf (Fig. 4), were responsible for the changes in species diversity indices (Fig. 5a and b).

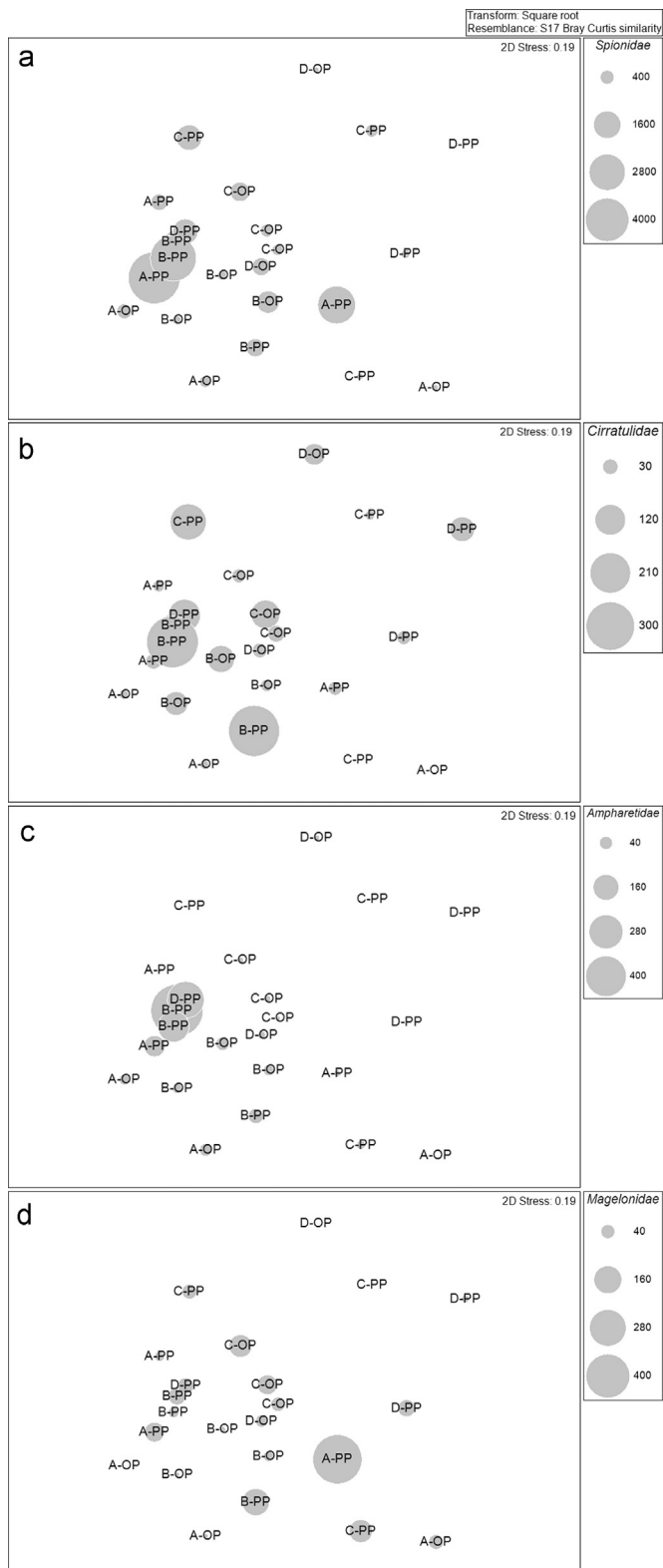


Fig. 4. Two-dimensional MDS plots of polychaete assemblages using square root transformed species abundance data (Bray–Curtis similarity) with superimposed bubbles indicating density of dominant polychaete families. (a) Spionidae, (b) Cirratulidae, (c) Ampharetidae and (d) Magelonidae at each site. Bubbles are labelled by depth (A: 30 m, B: 50 m, C: 100 m, D: 200 m) and monsoon phase (OP: onset phase, PP: peak phase).

3.4. Mature adults and juvenile polychaetes

Adult polychaetes bearing mature ova in their body cavity were

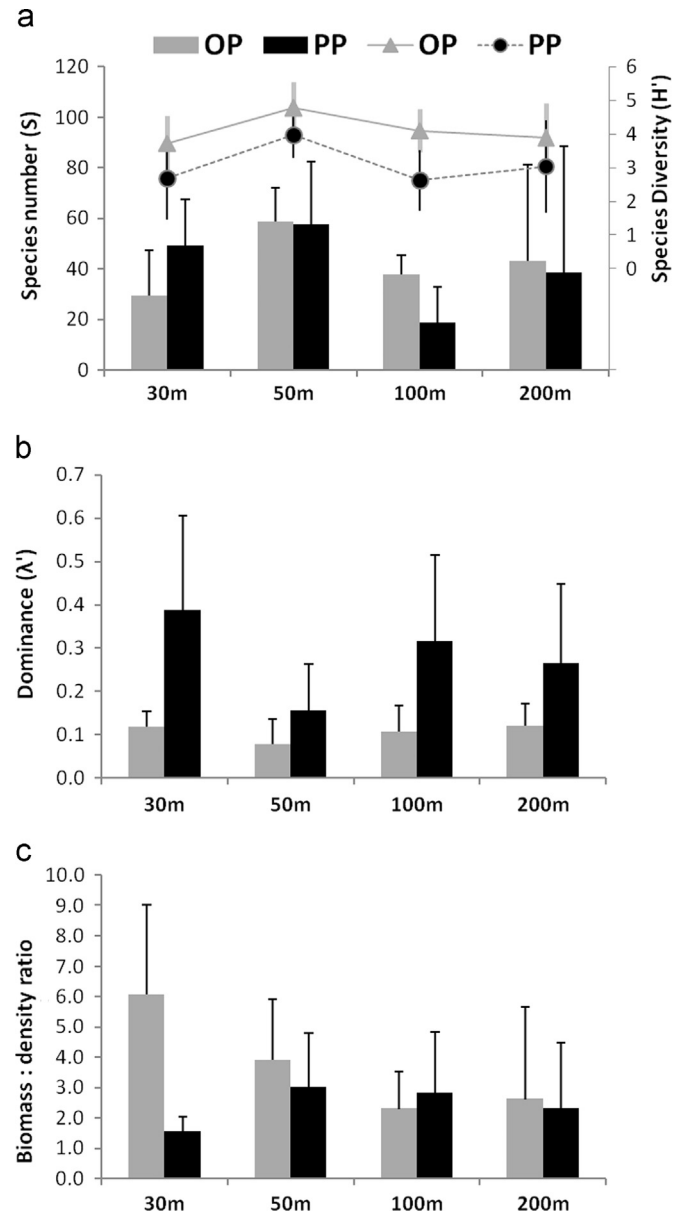


Fig. 5. Mean diversity indices and index of size of polychaetes (> 500 µm) at each depth stratum during the onset (OP) and peak phase (PP) of the southwest monsoon. (a) Species number, S (vertical bars + SD) and Shannon–Wiener Diversity, H' $\log_2$ (line graph + SD), (b) species dominance, λ' (+SD) and (c) biomass: abundance ratio (+SD).

retrieved from sediments during the OP and PP. During the OP, nine taxa belonging to seven families (Aphroditidae, Nephtyidae, Glyceridae, Lumbrineridae, Cirratulidae, Capitellidae and Terebellidae) were found in a gravid condition, while during the PP, mature ova were noted in eight taxa belonging to four families (Glyceridae, Spionidae, Capitellidae and Ampharetidae). The juveniles (small-sized forms) of several species were also found among the macrofauna during both surveys. These represented the post-settlement phases of polychaetes still to be retained in the 500 µm mesh (i.e. size > 500 µm), and belonged to families Pilargidae, Spionidae, Trochochaetidae, Amphinomidae, Glyceridae, Eunicidae, Ampharetidae and Terebellidae. The biomass: density ratios (mean individual body weight) decreased by ~50% at the 30 m sites during the PP (Fig. 5c), evincing the high numbers of these small-sized forms. High abundance of juvenile polychaetes (> 300 µm) was also noted during the late phase (LP) of the monsoon (2011).

Table 2

Mean density (range in parenthesis) of planktonic polychaetes during three phases of the southwest monsoon, 2009.

Month and Phase	Bongo net (surface haul)		MPN (vertical haul, entire water column)	
	Density (ind 10m ⁻³)	Families represented	Density (ind 10 m ⁻³)	Families represented
June – Onset phase (OP)	1824 (95–6107)	Spionidae (51%) Terebellidae (28%) Trochochaetidae (10%) Aphroditidae (6%)	75 (45–93)	Spionidae (36%) Ampharetidae (16%) Terebellidae (13%) Magelonidae (3%) Trochochaetidae (3%) Nereidae (1%) Others (28%)
August – Peak phase (PP)	16587 (0–65000)	Spionidae (73%) Others (26%)	348 (140–623)	Spionidae (76%) Pilargiidae (6%) Chaetopteridae (5%) Aphroditidae (5%) Magelonidae (1%) Spionidae (95%)
September – Late Phase (LP)	579 (0–2298)	Trochochaetidae (93%)	103 (0–152)	

3.5. Meroplanktonic polychaetes

Planktonic polychaetes were obtained at most sites during OP and PP, while they were obtained only at two sites along CAP transect during LP. In the surface haul (Bongo net), 86% (OP) and 96% (PP) of the polychaetes were larvae of benthic taxa, while the remaining were holoplanktonic forms. In the vertical column haul (MPN), 35% (OP) and 98% (PP) were meroplanktonic polychaetes. Density of larvae peaked during the PP, both in the surface water and the vertical column. Most larvae were in the nectochaete stage, but some large trochophores were also obtained. Density of larvae was higher in the surface when compared to the vertical haul, while more families were represented in the latter. Peak larval abundance in the PP was a result of high density of spionid larvae (86% of larvae in surface and 51% in vertical hauls). Larvae of nereids, terebellids and ampharetids were observed only in the OP, while larval pilargids and chaetopterids were encountered only in the PP. During the LP, only two families (Spionidae and Trochochaetidae) were represented among the meroplankton, with low density (Table 2).

4. Discussion

Physical oceanographic processes over the SEAS continental shelf during the southwest (summer) monsoon are dominated by coastal upwelling, which initiates towards mid-May, bringing cold, nutrient-rich, oxygen-deficient sub-surface waters to the surface, and results in enhanced biological production in the region (Bakun et al., 1998; Smitha et al., 2008; Jyothibabu et al. 2010; Thomas et al., 2013). Degradation of the vast quantities of OM in the sub-surface waters, and poor ventilation as a result of stratification, depletes oxygen from the already oxygen-poor upwelled water (Banse, 1959; Naqvi et al., 2009). Thus, towards the peak of the summer monsoon, the inner shelf sediments of the area are overlain with oxygen-deficient waters (Naqvi et al., 2009). Low bottom-water DO are reported along the shelf edge of the SEAS, as a result of the Arabian Sea OMZ (Joydas and Damodaran, 2014; Abdul Jaleel et al., 2014), and similarly low values ($\sim 0.5 \text{ ml l}^{-1}$) were recorded during both OP and PP surveys of the present study. The OM content was comparable to earlier observations in the region (Jayaraj et al., 2008; Joydas and Damodaran, 2014). High production during the southwest monsoon (Habeebrehman et al., 2008; Jyothibabu et al., 2010; Thomas et al., 2013) and terrestrial runoff could be expected to cause high OM load in the surface sediments. However, settlement of OM and finer particles to the

bottom is hindered by the dynamic currents operating in the SEAS during the period (Smitha et al., 2008), and this could explain the lack of significant temporal changes in sediment texture and OM content.

Nearshore sediments in the southwest coast of India are, in general, influenced by estuarine inputs (Nair and Hashimi, 1986; Jayaraj et al., 2008; Joydas and Damodaran, 2009), and the dominance of finer sediments at 30 m depth off Kollam (clay and silt together contributing $\sim 90\%$ in OP and PP) evinces such an influence by the Ashtamudi backwaters, where the heavier sediments remain trapped (Nair and Hashimi, 1986). The high proportion of silt during PP indicates the influx of substantial quantities of sediments from the backwaters during the monsoon season. The observations along the Kollam transect (30 and 100 m) provide evidence for the close relationship between OM content and sediment texture (Keil and Hedges, 1993; Abdul Jaleel et al., 2014).

The standing stock of macrofauna ($> 500 \mu\text{m}$) recorded during the present study fell within the range of values previously reported in the area (Jayaraj et al., 2008; Joydas and Damodaran, 2009, 2014), and a significant seasonal hike was noted in the inner shelf sediments (30 and 50 m) during the peak phase (PP) of the monsoon. Polychaetes and crustaceans were the dominant components during the onset phase (OP), being well suited to thrive in the sandy sediments of the SEAS shelf (Joydas and Damodaran, 2009, 2014). During the PP, when DO fell close to 0.2 ml l^{-1} at all sites (except CAP), the relative composition of these groups was altered significantly. Crustaceans, being less tolerant to low DO (Rosenberg et al., 1991; Diaz and Rosenberg, 1995; Grey et al., 2002), exhibited reduced abundance and biomass. At the 30 and 50 m sites along CAP, where DO remained relatively unchanged ($\sim 1\text{--}1.5 \text{ ml l}^{-1}$ during OP and PP), crustacean density did not change significantly. Along the shelf edge, where the Arabian Sea OMZ impinges on the sea floor, standing stock was much lower, and seasonal variations were not noticed (Joydas and Damodaran, 2014; Abdul Jaleel et al., 2014). With the reduction in density of crustaceans, and significant increase in polychaete density (particularly in the inner shelf), the relative composition of the latter group increased drastically in the PP ($\sim 90\%$ of macrofauna). The near absence of molluscs during the OP (pre-ban) may be due to the relative vulnerability of this group to physical disturbances such as trawling (Thrush et al., 1995; Collie et al., 2000; De Biasi, 2004; Dimitriadis et al., 2014). At the end of the 45 day trawling ban (PP survey), the density of this group increased, and they were represented at all sites.

The overall increase in density of polychaetes along the inner

shelf was a result of substantial increase in numbers of spionids, capitellids, cirratulids, pilargids, trochochaetids, amphinomids and ampharetids. These taxa (particularly genera *Paraprionospio*, *Prionospio*, *Linopherus*, *Tharyx* and *Notomastus*) are known to proliferate and establish themselves under low-oxygen conditions, often with high dominance (Levin, 2003; Joydas and Damodaran, 2009; Quiroga et al., 2007; Levin et al., 2009; Abdul Jaleel et al., 2014). Owing to dominance of these forms, species diversity in the PP was lower than the OP, despite a clear increase in species richness (S) at all but one site (KLM-50). A good proportion of these opportunists were accounted for by (small-sized) juveniles (particularly of *Paraprionospio* sp.1, *Prionospio* spp., *Linopherus* sp. 1, *Sigambra* spp. and ampharetids) along the inner shelf. This explains the lack of comparable increase in polychaete biomass, concurrent with the manifold increase in density.

Polychaetes have evolved diverse reproductive strategies, but broadcast spawning with planktotrophic or lecithotrophic larvae is typical, while direct development from embryos within the sediments are also not uncommon (Wilson, 1991; Eckelbarger and Watling, 1995; Hutchings, 1998). Opportunistic species, such as those mentioned above may breed year-round, but often show moderate to extreme seasonality in recruitment (Grassle, 1974; Yokoyama, 1995). In the eastern Arabian Sea, the breeding of several polychaete species is reported to coincide with the southwest monsoon (Thomas et al., 2006; Sivadas et al., 2010; Bhagirathan et al., 2014). Breeding populations of some free-spawning (planktotrophic and lecithotrophic) species occurred within the sediments during the study. Juveniles of free-spawning as well as direct-developing forms were also present in the sediments, and these dominated along the inner shelf during the PP. Polychaetes appear to take advantage of the seasonal pulses in production during the monsoon (Habeebrehman et al., 2008; Jyothibabu et al., 2010; Thomas et al., 2013), by synchronizing vitellogenesis (in the case of lecithotrophic larvae) or spawning (planktotrophic larvae) with the peak in regional biological production (Gooday, 2002).

Planktonic larval abundances were highest during the peak of the summer monsoon, and the bulk of larvae belonged to Spionidae. Even though this family shows a variety of recruitment modes (even within the same species), free spawning with free-swimming planktotrophic larvae is most common (Levin, 1984; Wilson, 1991). The proliferation of smaller-sized diatoms during the beginning of the southwest monsoon in the SEAS (Thomas et al., 2013) provide ideal food sources for the planktotrophic larvae of polychaetes. The density of larvae decreased sharply in the late monsoon, during which season, smaller-sized (juvenile) polychaetes were abundant in the sediments (LP). Despite variability in the timing of spawning and settlement, it is generally believed that peaks in abundance of planktonic larvae are reliable predictors of temporal windows for recruitment among polychaetes (Feller et al., 1992).

The settlement of polychaete larvae is a dynamic event, with larvae actively rejecting inhospitable sites and selecting most suitable substrates (Crisp, 1974; Pawlik, 1992). Active site selection can be mediated by environmental and biological triggers, which include chemical cues from conspecific and congeneric individuals, and also prey species and sympatric species (Qian, 1999). It is asserted that stable environments and sea beds, along with the presence of adults of the same species will result in larval settlement at that site, and reduce post settlement mortality as well. The lack of (direct and indirect) trawling disturbances between June and August (trawl-ban period), thus, may enhance settlement of larvae in an environment which is already subjected to natural stress (low oxygen conditions). This is evinced by the presence of juveniles of many species towards the end of the trawl-ban period and during the late phase of the monsoon. The

alleviation of disturbance may also provide better protection to breeding populations in the sediments, from the direct deleterious effects of trawling.

Trawling is well known to affect not only standing stock, but also diversity and community composition of benthic invertebrates, either due to the immediate mortality inflicted by trawling gear or the long-term ability of populations to cope with this mortality (Dayton et al., 1995; Jennings and Kaiser, 1998; Hall, 1999; Collie et al., 2000; Kaiser and deGroot, 2000; Jennings et al., 2001). The temporary cessation of trawling disturbances (trawl-ban) may be responsible for increase in polychaete species richness in the SEAS shelf, despite the low-oxygen conditions, which is otherwise known to cause depression of richness and diversity (Levin, 2003; Levin et al., 2009). Similarly, molluscs, which are most vulnerable to physical impacts of trawling (Thrush et al., 1995; Collie et al., 2000; De Biasi, 2004), were also able to recover within the 45-day trawl-ban period.

The impact of trawling on benthic communities can vary widely, depending on a variety of factors including nature and scale of trawling, nature of bottom, depth and season. In a tropical developing country like India, where fishing effort is reasonably high, maritime states impose a seasonal trawling ban in order to ease stress, not only on fishery resources, but also on benthic communities that support them. Off the southwest coast of India, in the south eastern Arabian Sea (SEAS), this ban falls between June 15th and July 30th each year and coincides with the onset of the southwest (summer) monsoon. A recoupment of macrobenthic standing stock was evident in this region, within this 45 day period. This was found to be a direct result of recruitment of certain species, which also form the chief resident fauna of the region. These species appear to synchronise their breeding with the high biological production in the region during the monsoon. The trawl-ban may provide protection to the breeding populations of these species within the sediments, and also enhance the settlement of their larvae which resulted in their dominance in sediments towards the peak monsoon. Apart from proliferation of these forms, polychaete species richness also recorded an increase, as did the density of molluscs. The standing stock and community structure of macrofauna in the SEAS is subject to seasonal variation, chiefly under the influence of the summer monsoon and coastal upwelling. The trawling ban in this region is favourably timed to coincide with the period of high biological production, which is asserted to be a major breeding window of its resident polychaete fauna. Thus, the ban has an overall positive effect on the benthic ecosystem, which may presumably be conveyed across trophic levels, and prove beneficial for demersal fishery.

5. Conclusions

The macrobenthic standing stock showed considerable recoupment during the 45 day monsoon trawling ban (June–July) in the southern part of the southeast Arabian Sea shelf, particularly between 30–50 m depths. A peak recruitment window for the dominant polychaete taxa in the region is identified around the onset and peak phases of the monsoon, as inferred from the gravid adults in sediments and increase in meroplankton densities. This recruitment event was found to enhance density and biomass of polychaetes, and is responsible for a dominance of juveniles in the sediments towards the peak of the monsoon, which coincides with the end of the trawl-ban. The standing stock along the outer shelf (100–200 m), did not record significant enhancement during this season, owing to the bottom-water hypoxia which prevailed here. Polychaete species richness in the region was also boosted across the trawl-ban period. The synchronization of recruitment with the southwest monsoon-associated high biological production

enhances reproductive success of major polychaete taxa, which is further augmented by the absence of physical disturbances by trawling in the SEAS shelf.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.csr.2015.04.011>.

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